# Geomorphic Controls of Spatial Pattern and Process at Alpine Treeline*

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This study examines the role of surface geomorphic features in tree establishment at the alpine treeline in Glacier National Park, Montana, through the presentation of a multiscale, conceptual model of biogeomorphic relationships at alpine treeline. Empirical observations gathered through a multiscale field methodology over three summers serve as a base for the model. The model highlights the importance of surface geomorphic features, specifically boulders and terrace risers, in creating favorable local site conditions, largely by protecting seedlings from wind. The sheltering effect of surface features enables initial seedling establishment, and in some cases survival, above current treeline locations, thereby initiating a positive feedback effect that encourages subsequent tree establishment. Geomorphic features are therefore important in linking scales of pattern and process at the alpine treeline ecotone. **Key Words: alpine treeline, biogeomorphology, Glacier National Park, mountain environments, seedling establishment.**

Alpine treeline, the zone of transition between closed forest and open tundra, is arguably the most discernible landscape boundary in the American West. At alpine treeline, both subalpine and alpine species are close to their climatic distribution limits (Walsh, Malanson, and Butler 1992; Rochefort et al. 1994; Malanson et al. 2002). This prominent boundary represents the upper elevational limit to tree growth on mountain slopes, and is therefore an important ecological threshold. Above this threshold, large single stems and tall crowns of trees become disadvantageous and therefore are replaced with the more advantageous life forms found in the true alpine environment (Tranquillini 1979; Körner 1999). The spatial pattern of the alpine treeline ecotone is characterized by closed forest in lower elevations, which breaks up into patches of tree islands and individual trees before being replaced completely by tundra vegetation.

The location and pattern of alpine treeline result from the combined influence of a number of environmental (Daubenmire 1954; Gloyne 1955; W. J. Wilson 1959; Wardle 1974; Tranquillini 1979; Arno and Hammerly 1984; Hadley and Smith 1986; Innes 1991; Körner 1999; Cairns 2001; Alftine 2002) and biological (Tranquillini 1979; Arno and Hammerly 1984; Cairns and Malanson 1997; Körner 1998, 1999; Hoch and Körner 2003) variables that covary in complex and nonlinear ways (T. F. H. Allen and Starr 1982; T. F. H. Allen and Hoekstra 1992; Delcourt and Delcourt 1992; Brown et al. 1994; Rochefort et al. 1994; Malanson 1999). Physiological processes underlie the observable variation in tree performance and operate in complex ways with environmental factors to determine the overall spatial pattern of alpine treeline (Svienbjörnsson, Hofgaard, and Lloyd 2002). Therefore, both site factors and plant performance are important to consider when evaluating patterns of conifer establishment at treeline.

In addition to environmental and biotic variables, treeline research in the area of biogeomorphology has established the importance of geomorphic processes on the position and pattern of alpine treeline. Most studies of the

relationship between geomorphic controls and alpine vegetation have emphasized the constraining character of geomorphic processes and lithologic controls (Butler and Walsh 1990, 1994; Walsh et al. 1990; Walsh, Butler, and Malanson 1997) and the distribution of snow (T. R. Allen and Walsh 1993, 1996; Rochefort et al. 1994; Walsh et al. 1994) on treeline at a landscape scale.

Despite the attention given to the geomorphic constraints of treeline, few studies have examined in detail the potential that geomorphic aspects may facilitate treeline advance—a perspective that necessitates a multiscale approach to understanding links between pattern and process at treeline. Walsh, Butler, et al. (2003) explored the geomorphic benefits to tree growth at the alpine treeline ecotone from a GIS-based perspective; Bekker (2005) noted the potential importance of surface geomorphic features in aiding treeline advance; and Butler, Malanson, and Resler (2004) clearly linked microscale turf exfoliation to individual conifer establishment. However, Resler, Butler, and Malanson (2005) have provided the first empirically rich dataset for investigating the specifics of tree growth at treeline from the perspective of geomorphic controls. This work establishes the importance of surface geomorphic features, such as boulders and terrace treads and risers, in influencing the spatial structure and advance of alpine treeline. Surface microtopography provides shelter from wind, thereby improving local site conditions that increase seedling establishment and survival in the most exposed locations of the alpine treeline ecotone.

The purpose of this study is to propose a conceptual model that describes the multi-spatial-scale relationship between treeline advance and geomorphology. The approach examines the spatial patterns of tree occurrence at three spatial scales to establish the relative roles of macro- (landscape scale), meso- (aspect and elevation), and microscale (level of individual tree growth, establishment, and death) controls on tree establishment at the highest locations of alpine treeline. This research relies on the rich empirical observations presented in Resler, Butler, and Malanson (2005) and a synthesis of work conducted by treeline researchers worldwide, but it specifically highlights work conducted in Glacier National Park. In addition, new soils data are presented. These data are used to more

fully address fine-scale controlling mechanisms of treeline. The basis for this model relies on answers to the specific research questions listed in Table 1.

The model of treeline presented here expands on two innovative and interrelated biogeomorphic concepts: (1) the role of geomorphology in aiding treeline advance, informed by the concept of positive feedback, and (2) the role of geomorphology in linking scale of pattern and process at treeline, informed by hierarchy theory.

Positive feedback mechanisms and the importance of shelter as a modifying agent place the role of geomorphology in aiding treeline advance in theoretical context. The concept of a positive feedback refers to a process where a community modifies the environment it occupies (J. B. Wilson and Agnew 1992). The impact of such positive feedback mechanisms in shaping ecological patterns is well documented for both alpine, arctic, and desert environments (Marr 1977; Benedict 1984; Pérez 1987, 1991, 2002; K. C. Parker 1989; Svienbjörnsson, Hofgaard, and Lloyd 2002; Alftine, Malanson, and Fagre 2003; Alftine and Malanson 2004; Bekker 2005).

Microtopography is important in improving local site conditions that increase seedling establishment and survival in the most exposed

**Table 1** *Research questions used to build a biogeographic model of treeline advance*

**Microscale research questions**

1. Are live conifers found to be close spatial associates with periglacial geomorphic features at alpine treeline?[a]
2. Do live conifers associated with shelter exhibit a preference for a particular type of shelter?[a]
3. How do shelter types vary in terms of the quality of protection offered, as evidenced by conifer mortality?[a]
4. What are the local patterns of soil penetrability and soil depth in and around conifer establishment sites?[b]

**Mesoscale research questions**

1. How is the density of conifers or conifer patches influenced by elevation among the three study sites?[b]
2. Does elevation influence species richness among the three study sites?[b]

**Macroscale research questions**

1. What kind of periglacial shelters are available among the three study sites?[a]
2. Do species vary among the three study sites?[a]
3. Does site richness vary among the three study sites?[a]

[a]*Data and results presented in Resler, Butler, and Malanson (2005).*
[b]*Data and results presented in the current paper.*

locations of the ecotone. Periglacial shelters locally lower temperatures, offer protection from wind, influence soil conditions, and serve as seed traps (Marr 1977; Carlsson and Callaghan 1991; Nuñez, Aizen, and Ezcurra 1999; E. R. Parker and Sanford 1999; Callaway et al. 2002; Resler, Butler, and Malanson 2005). From an abiotic perspective, modifications of microclimate through tree establishment and subsequent growth could enable additional trees to grow at increasingly high elevations or exposed locales (Smith et al. 2003). Surface microtopography can therefore play an important role in seedling establishment and survival, which are necessary for treeline advance, observable on a landscape-scale, to take place.

Second, the connections in the model presented here rely on the idea that geomorphology plays an important role in linking pattern and process at alpine treeline, an idea grounded in the concept of ecological hierarchy. The main premise underlying hierarchy theory is that broader scales give insight into spatial patterns, or ecological context, and finer scales give understanding into the explanatory mechanisms that structure that pattern (T. F. H. Allen and Starr 1982; T. F. H. Allen and Hoekstra 1992). Additionally, all ecosystems and processes therein may be observed from multiple spatial and temporal scales, and scale is fixed only within the context of observation and measurement (T. F. H. Allen and Hoekstra 1992).

Because there exist relationships among ecological levels, is it important to consider both coarse and fine scales in biogeographic analyses. For example, the pattern at alpine treeline observed from a landscape scale (context) may best be understood by investigating the controlling factors of individual tree establishment (mechanism). At treeline, the macroscale (landscape scale) response of mountain vegetation to fluctuations in temperatures during the Holocene has been historically manifested as upward shifts of general treeline position as a response to warmer climates, with lower-elevation treelines forming as a response to cooler climates (Rochefort et al. 1994; Lloyd and Graumlich 1997). However, this general trend may not always be observable at a landscape scale because microscale factors, such as the growth and death of individual trees, and microscale conditions, such as boundary layer climates, also help determine the extent and nature of treeline shift.

For example, research incorporating analysis of ground-based and aerial photographs (Butler, Malanson, and Cairns 1994; Klasner and Fagre 2002) show a general lack of upward movement of treeline at Glacier National Park; however, using a detailed field approach Bekker (2005) reported evidence of infilling and treeline advance.

## Study Site and Method

This research is a natural extension of the work presented in Resler, Butler, and Malanson (2005). This section describes the study site and method used to obtain data for the new analysis presented in this study and the collection of specific geomorphic data presented in the aforementioned article.

### Study Sites

Climate-inspired investigations of change at alpine treeline are best conducted within protected settings where human impacts are controlled and at a minimum. Glacier National Park provides an ideal setting for this research because of its relatively pristine alpine environment in which human impacts at treeline have been minimal since the park's inception in 1910. Within the Park, three study sites are used: Lee Ridge, Cataract Creek Basin, and Divide Peak, all located east of the Continental Divide where the climate is drier, windier, and cooler than climates west of the Divide (Finklin 1986; Walsh, Malanson, and Butler 1992; Figure 1). Accessibility and the existence of relict solifluction terrace treads and risers, which are step-like, linear, patterned-ground formations created by accumulations of fine-grained material (Washburn 1980; Butler and Malanson 1989, 1999), governed the selection of the sites. These three sites represent some of the most abiotically stressful environments where conifers grow in this region. Surface boulders that have been transported from cliff bases by the flow of previously active solifluction scatter the landscape. Although terrace treads and risers are found throughout each site, boulders as a shelter source are not as evenly distributed due to variation in proximity of sites to cliff bases. Site characteristics of each study site are listed in Table 2.

There are several advantages to choosing study sites associated with periglacial landscapes. First, knowledge of past geomorphic activity on

**Figure 1** *Study sites in eastern Glacier National Park.*
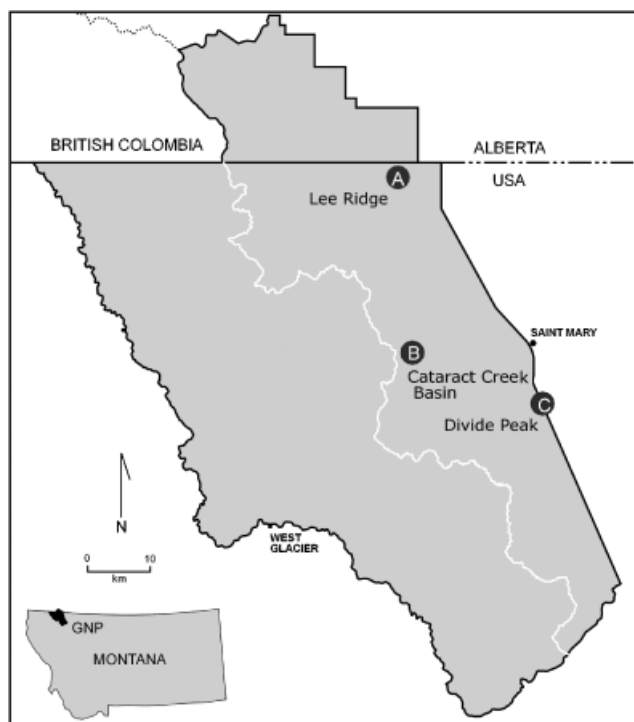
these sites provides a benchmark from which to estimate treeline movement. At all three sites, solifluction is inactive under present climatic conditions, and trees were not likely to form on its surface when it was active. Second, the sites did not undergo glaciation during the Little Ice Age, and therefore are characterized by gently sloping topography rather than steep slopes where the distribution of trees may be affected by slope instability or geomorphic activity. Third, periglacial landscapes such as those found on the eastern slopes of GNP, by their topographic nature, are characterized by an abundance of microtopographic features that may serve as shelter to conifers. Figure 2 depicts a boulder that provides leeward shelter to conifers from the prevailing westerly winds, with relict solifluction terrace treads and risers in the back-

ground. Characteristics of the relict solifluction terrace treads and risers are detailed in Butler and Malanson (1989, 1999), Walsh, Butler, et al. (2003), and Walsh, Bian, et al. (2003).

Primary response of alpine treeline in Glacier National Park to climatic warming after the Little Ice Age (ca. 1850 A.D. in the park) has been an increase in tree density, rather than a measurable landscape scale shift in the elevation of alpine treeline (Butler, Malanson, and Cairns 1994; Klasner and Fagre 2002). Using dendro-chronology, Bekker (2005) determined that the beginning of the most recent forest advance predated the end of the Little Ice Age, albeit slowly, in the eighteenth century, and it accelerated during the late 1800s. New seedlings have established at alpine sites in the park within the past fifty years (Alftine and Malanson 2004).

**Table 2** *Characteristics of study sites, Glacier National Park*

|  | Lee Ridge | Cataract Creek Basin | Divide Peak |
|---|---|---|---|
| Elevation range | 2028–2146 m | 1965–2103 m | 2040–2115 m |
| Azimuth/aspect slope range | 330°–350°/NNW 6°–16° | 274°–336°/NNW 10°–18° | 324°–27°/NNW-NNE 5°–16° |
| Parent material | Altyn limestone | Siyeh limestone (Helena Formation) | Altyn limestone |

**Figure 2**  *Periglacial landscape at alpine treeline, Lee Ridge, Glacier National Park, Montana. Note establishment of conifers in lee of boulder shelter.*

Whereas each site is characterized by similar microtopography, macrotopographic settings among the sites differ (Figure 3). Differences in macrotopography among sites are important in terms of influencing wind speeds and direction at each site through topographic channeling. Lee Ridge is an isolated, exposed ridge located perpendicular to the prevailing westerly winds. Cataract Creek Basin is situated at the base of a cirque headwall close to the Continental Divide, where wind is channeled down the cirque from over the pass at the head of the cirque. The Divide Peak site is located on inactive solifluction treads and risers at the base of an isolated peak at the easternmost boundary of the Rocky Mountain physiographic province. This site becomes increasingly subject to wind-exposed conditions farther away from the base of the peak.
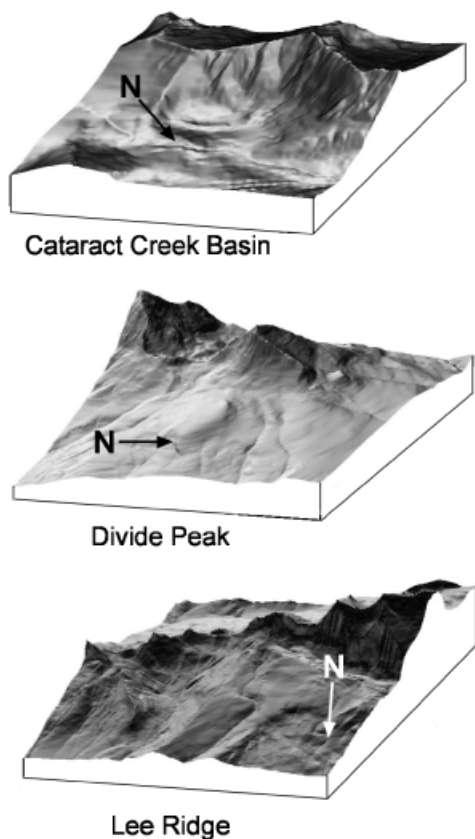
An elevation gradient of vegetation forms and species is apparent in Glacier National Park, with lower subalpine forests dominated by *Picea engelmannii* and *Abies lasiocarpa*. Tree species of alpine treeline on the east side of the Continental Divide include *Abies lasiocarpa*, *Picea engelmannii*, *Pseudotsuga menziesii*, *Pinus albicaulis*, *Pinus flexilis*, and even *Larix lyallii* in locations close to the Canadian border. Dwarf conifer shrubs include *Juniperus communis* and *Juniperus horizontalis*. Wind is an important climate variable affecting the local pattern of these treeline species (Grace 1977, 1989; Alftine and Malan-

son 2004) through the creation of tree islands and distribution of snow (Alftine, Malanson, and Fagre 2003). Many trees at the study sites are separate individuals, established from seed rather than through layering (Bekker 2005). However, at higher elevations at Lee Ridge and Cataract Creek Basin, there are trees that reproduce primarily through layering.

### Field Methods

The goal of the larger work on which this model is based was to assess geomorphic influences on treeline dynamics across spatial scales. Therefore, detailed characteristics of conifer establishment sites characterized by a single conifer or conifer patch with multiple individuals, and their immediate spatial environments, were observed using field-based techniques and were examined within their larger scale topographic and regional context. Fieldwork took place over a period of three summers from 2001–2003. Resler, Butler, and Malanson (2005) detail these measurements.

In the study sites, conifers exist as patches or isolated individuals at the extremes of their distributions and are associated with periglacial features such as terrace risers or boulders. The patches are landscape elements distinct from continuous forest cover that can be found downslope. Using the quadrat method, such microsites were identified for sampling. At each

and Malanson (2005) do not necessarily shed light on individual seedlings that might establish on the vertical face of a cliff in a joint fracture or on glacial moraines, which are environments controlled by disturbances resulting from unconsolidated material.

In each elevation zone, one $30 \times 30$ m quadrat was randomly positioned for a total of fifteen quadrats, five at each study site. The five quadrats at each macroscale study site helped to capture mesoscale variation due to elevation in conifer establishment. Quadrats delineated space to measure microscale aspects of conifer establishment, and a total of 211 conifer microsites were identified and measured using this method (Resler, Butler, and Malanson 2005). Microscale variables included presence/absence of shelter, shelter type, vegetation height, soil penetrability and depth, species composition, and conifer mortality. Macroscale variables were site-specific variables: species richness, and macroscale topographic characteristics. Conifer species richness referred to the total number of conifer species per regional study site. Density per site was calculated by counting the number of conifers patches per quadrat, then converting into the number of conifer patches per hectare.

Soil penetrability, a measure of compaction, is a potentially important characteristic of soils that may indicate moisture available to plants, and the ability of a seed to implant itself into the soil and to germinate. High penetrability values suggest poor permeability, and therefore low values on the soil penetrometer imply conditions conducive to seedling establishment. On a total of eighty microsites from the three study site locations, soil penetrability was measured three times at each of five locations relative to the microsite: leeward of the patch, upslope from the patch, downslope from the patch, windward of the shelter, and center of the patch (Figure 4). To sample soil penetrability, a soil penetrometer was used to take three measurements. This method yielded a total of 1,200 soil penetrability measurements.

Soil depth is potentially important to tree growth because it can limit the amount of water available (Cairns and Malanson 1998). Although tundra soils are deep enough for seedlings to become established (Schmid 2004), modification of soil depth by tree establishment could enhance the ability of seedlings to become established in small protected microsites. Soil



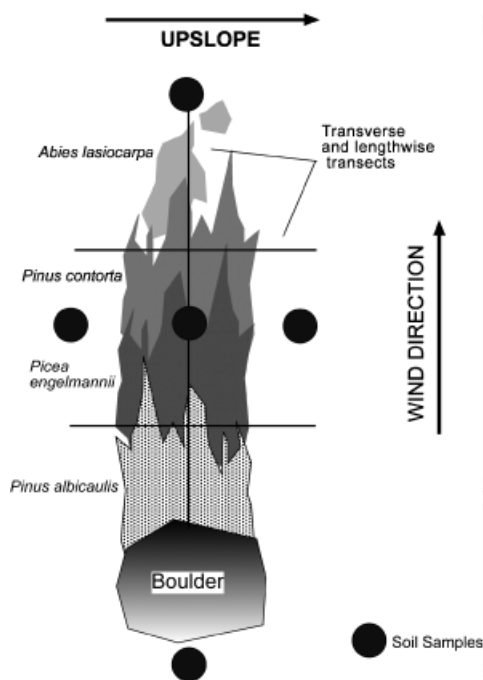**Figure 3**  *Macrotopographic context for the three study sites.*

of the three macroscale study sites, five elevation zones above closed treeline were identified to examine trees growing in exposed locations. The elevation zones are approximately 100–150 m of the highest elevations where conifers, often in the form of dwarfed trees and krummholz, grow on periglacial sites. Trees exist at higher elevations on the west side of the park where the climate is more moderate; however, these higher trees were omitted from consideration for the study because of the desire to keep the microclimates as uniform as possible. The study was also limited to locations where tree seedlings are invading relict periglacial sites, characterized by turf-banked treads and risers. These periglacial features are among the most common and spatially extensive landform categories found immediately adjacent to treeline (Carrara 1990). The findings in this study and in Resler, Butler,

**Figure 4** *Detailed microsite sampling plan.*

depth may be deeper in the lee of a boulder than it is in the exposed tundra, which is a function of the ability of a boulder to act as a sediment and moisture trap. Variability of soil depth in different positions around a microsite should indicate the ability of a vegetation patch to modify soil depth in its local area, and distinguish it from tundra soil depth. Measurements of effective soil depth, an indicator of stoniness and root potential root depth penetration, followed the same design as soil penetrability. A steel rod was pushed into the ground three times to capture soil depth; the deepest of the three measurements served as the recorded effective soil depth (Ericksson and Holmgren 1996; Malanson et al. 2002). In total, 400 total soil depth measurements were collected.

## Results

Local soil conditions, perpetuated by the growth of trees in positive feedback cycles, may be important for initial establishment of conifers. A one-way ANOVA was used to assess whether the means of the dependent variables, effective soil depth and soil penetrability, differed significant-

ly by location in and around the conifer patch. Although variability was found within patches regarding the spatial distribution of soil resources, soil depth and soil penetrability were significantly higher ($p < 0.05$) in the center position where plants are growing, than at the windward side, where plants were not found to grow, or at the leeward edge of the patch, upslope or downslope (Table 3). This pattern was similar at all three sites, with the exception of soil depth at Cataract Creek Basin, where no significant differences were found between effective soil depth and location. Even though Cataract Creek Basin did not show significantly different effective soil depth in the patch center from other patch locations, it still had a higher mean than other patch locations. Intense wind speeds that may influence seed dispersal and germination, combined with a high slope gradient, could cause the lack of significant variation in soil depth with microsite position at Cataract Creek Basin, but positive feedback mechanisms between plants and soil are likely present.

Hypotheses that tested density of conifer sites with elevation, species richness with elevation, revealed different results among the sites. Density of conifer sites (number of conifers per hectare) with elevation varied among study sites. The negative correlation between conifer density and elevation was significant and strong ($r = -0.90, p < 0.05$) at Divide Peak. At all other sites, and for the general trend among the three sites, there were no significant correlations found between conifer density and elevation. A significant, but weak correlation between elevation and species richness was found only at Lee Ridge ($r = -0.36, p < 0.05$). Species found at each site and species richness varied among different site types. Lee Ridge had the highest species richness, with seven conifer species; Cataract Creek Basin and Divide Peak each had five conifer species diversity, despite its proximity to the Continental Divide, where seed from both eastern and western tree species should be available (Resler, Butler, and Malanson 2005).

## A Biogeomorphic Approach to Linking Scale of Pattern and Process at Alpine Treeline

The purpose of this study was to gain an understanding of the role of surface geomorphic

**Table 3**  ANOVA results (soil depth and soil penetrability) for Lee Ridge, Divide Peak, and Cataract Creek Basin

| Mean soil depth (cm) | F-Value, p-Value | Windward | | Upslope | | Downslope | | Leeward | | Center | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | Standard deviation | Mean | Standard deviation | Mean | Standard deviation | Mean | Standard deviation | Mean | Standard deviation |
| Cataract Creek Basin | $F = 1.86$ $p > 0.12$ | 15.5 | 8.4 | 6.3 | 8.5 | 15.8 | 9.1 | 16.0 | 8.7 | 20.6 | 7.2 |
| Divide Peak | $F = 6.43$, $p < 0.001$ | 15.6 | 7.0 | 13.0 | 7.7 | 17.8 | 8.8 | 14.6 | 7.6 | 23.8 | 9.2 |
| Lee Ridge | $F = 5.11$, $p < 0.001$ | 15.9 | 8.2 | 13.8 | 7.5 | 16.6 | 9.0 | 12.9 | 7.5 | 22.0 | 8.5 |
| **Mean soil penetrability (kg/cm$^2$)** | | | | | | | | | | | |
| Cataract Creek Basin | $F = 22.52$, $p < 0.001$ | 1.8 | 0.7 | 1.8 | 0.7 | 1.6 | 0.7 | 1.5 | 0.7 | 0.9 | 0.4 |
| Divide Peak | $F = 27.31$, $p < 0.001$ | 2.0 | 1.0 | 2.3 | 0.8 | 2.1 | 0.8 | 2.2 | 0.9 | 1.0 | 0.5 |
| Lee Ridge | $F = 20.19$, $p < 0.001$ | 1.8 | 0.8 | 1.9 | 0.9 | 1.7 | 0.7 | 1.7 | 0.7 | 1.0 | 0.5 |

features in aiding treeline advance in Glacier National Park from a multiscale perspective. Results presented in this study and in Resler, Butler, and Malanson (2005) highlight the importance of microscale factors, such as shelter, and conifer establishment, at three study sites in Glacier National Park. However, when examining meso- and macroscale factors, such as the relationship between conifer density and elevation, geographic variability among the sites is apparent. These observations raise important questions about scale linkages at alpine treeline.

The relationship between pattern and process vary in a complex manner with scale (T. F. H. Allen and Hoekstra 1992; Malanson 1999). A common problem is that the mechanisms producing a pattern operate at a different scale than the scale at which the pattern is observed (Levin 1992; Brown et al. 1994). Hierarchy theory conceptualizes the environment and interactions between the entities in the ecological universe into levels of organization, or scales of organization, that range from the cell to the biosphere (T. F. H. Allen and Hoekstra 1992). The main premise underlying hierarchy theory is that broader scales give insight into spatial patterns, or ecological context, and finer scales give understanding into the explanatory mechanisms that structure that pattern (T. F. H. Allen and Starr 1982; T. F. H. Allen and Hoekstra 1992). Additionally, all ecosystems and processes therein may be observed from multiple spatial and temporal scales, and scale is fixed only within the context of observation and measurement (T. F. H. Allen and Hoekstra 1992).
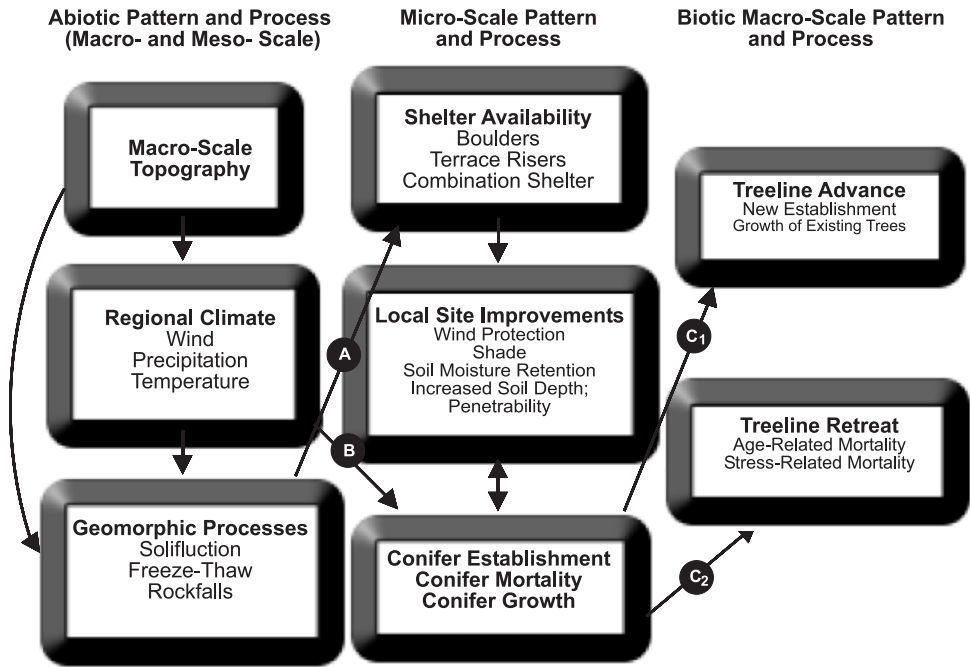
Based on the notion of hierarchy theory and positive feedback, surface geomorphology plays an important role in linking pattern and process among scales at alpine treeline in Glacier National Park for two primary and interrelated reasons. First, shelter reduces exposure to wind. Second, improved site conditions as a result of this sheltering effect initiate positive feedbacks. As trees become established, their presence modifies the local environment and makes local conditions more favorable for additional seedlings to grow.

These important connections among biogeographic and geomorphic elements at alpine treeline are put into a visual framework in Figure 5. The model describes how treeline dynamics, including both advance and retreat, are influenced by a complex set of abiotic and biotic variables with surface geomorphic features occupying a central role in linking scales of pattern and process at treeline. The discussion centers on links A, B, and C.

*Link A: Geomorphic Slope Processes (Box 1) to Shelter Availability (Box 2)*

In mountainous areas, geomorphic slope processes such as solifluction, rockfalls, debris flows, and freeze-thaw processes are prevalent. Regional climate, especially temperature and precipitation, influence geomorphic processes. Transport of material downslope (e.g., boulders) through creep and flow processes, can

**Abiotic Pattern and Process (Macro- and Meso- Scale)**

**Micro-Scale Pattern and Process**

**Biotic Macro-Scale Pattern and Process**

**Macro-Scale Topography**

**Shelter Availability**
Boulders
Terrace Risers
Combination Shelter

**Treeline Advance**
New Establishment
Growth of Existing Trees

**Regional Climate**
Wind
Precipitation
Temperature

**Local Site Improvements**
Wind Protection
Shade
Soil Moisture Retention
Increased Soil Depth;
Penetrability

A

B

C₁

**Treeline Retreat**
Age-Related Mortality
Stress-Related Mortality

**Geomorphic Processes**
Solifluction
Freeze-Thaw
Rockfalls

**Conifer Establishment
Conifer Mortality
Conifer Growth**

C₂

**Figure 5**   *A biogeomorphic approach to treeline dynamics.*

provide seedlings with potential habitat for establishment and survival. For example, the three major shelter types found to exist in association with conifer establishment on the eastern slopes of Glacier National Park are associated with these types of large-scale geomorphic processes. Research has shown that seedling establishment in Glacier National Park is associated with such shelter. Resler, Butler, and Malanson (2005) found a significant spatial association between conifer growth above treeline and available shelter at the sites: terrace risers, boulders, and combination shelters, which included both boulder groups and riser/boulder combination shelters. Only five conifers total out of the 211 sampled were not associated with shelter, highlighting the importance of shelter in tree establishment above treeline. Additionally, Butler, Malanson, and Resler (2004) found a positive association between seedling establishment and turf exfoliation sites. Such patterns have been noted in other alpine areas as well. For example, Pérez (1987) noted that large alpine rosettes found at a Northern Andes treeline are close spatial associates with rocky outcrops, crevices, fissures, and boulders.

Such close spatial associations between conifer establishment sites and microtopography are indicative of positive, or beneficial, associations (K. Parker 1989; Callaway 1995). Indications of positive feedback were found in the close spatial associations between conifers and shelter. These results are consistent with theories relating to the relative important of competition versus facilitation in shaping landscape patterns along environmental gradients. Along a gradient of increasing abiotic stress, facilitation has been found to increase in importance as plants' physiological limitations increase (Callaway et al. 2002). Limiting factors of plant growth at treeline include temperature, wind scouring, and soil instability due to freeze-thaw processes. These limiting abiotic factors are ameliorated through the effects of periglacial microtopography and the facilitating effects of other trees. At the three study sites addressed in this paper, positive feedbacks associated with patterns at the alpine treeline ecotone may originate from the establishment of a seedling in a favorable location, such as behind a boulder, in the shelter of a solifluction riser, or behind another plant.

Shelter, such as surface microtopography, can locally improve site conditions for treeline conifers in a number of ways. These benefits include locally moderating temperatures, providing protection to plants from severe weather and wind, influencing soil conditions, and serving as seed traps (Marr 1977; Carlsson and Callaghan 1991; Nuñez, Aizen, and Ezcurra 1999; E. R. Parker and Sanford 1999). Microtopography may play an important role in the modification of microclimates near mountain timberlines (Billings and Mark 1961; Barry 1992; Körner 1999; Anderson and Bliss 1998). From their observations in the Northwest Territories, Anderson and Bliss (1998) noted that the influence of rocks on microscale environmental gradients associated with patterned ground had an influence on stabilizing soils and determining the spatial distributions of vascular plants. Boulders and surface stones increase the water-holding capacity of soils (Lamb and Chapman 1943; Pérez 1987, 1991; K. Parker 1989), reduce erosion (Lamb and Chapman 1943), provide impact protection on steep slopes (Pérez 1991), provide soil stabilization (Anderson and Bliss 1998), and create shade and wind barriers (K. Parker 1989). Vegetation that establishes in microsites improves site conditions by reducing wind speed by 80 percent up to 3–5 times the height of the vegetation downwind. These processes generate distinctive patterns of tree islands that form in the lee of a sheltered site, often in a cushion growth form (Wardle 1974; Grace 1977; Marr 1977; Benedict 1984; Barry 1992). Establishment and subsequent survival in topographically-controlled microsites may influence the patchy nature of vegetation at the alpine treeline ecotone (Holtmeier and Broll 1992; Nuñez, Aizen, and Ezcurra 1999).

Finally, isolated boulders on an open landscape may affect the boundary layer climates of the area. Acting as roughness elements on the surface, boulders and associated vegetation create turbulence in the air layers and thus at night transfer heat from warmer layers above a snow-covered surface to the colder layers below. This affect causes a warm area downwind of the roughness element (Oke 1978). These local site improvements may allow additional individuals that otherwise would not have a competitive advantage to become established (Marr 1977; Benedict 1984; Walker, Billings, and DeMolenaar 2001).

Once a tree becomes established and grows in a favorable site behind a rock or in the shelter of small surface irregularities, the growing tree creates a positive feedback that improves the soil and reinforces wind protection. Plants influence soil formation through the addition of organic material and increasing soil penetrability (Pérez 1995). Local variability and patterns of organic matter and soil penetrability found around the conifer patches in this study suggest that positive feedback effects are operating within conifer patches. Although variability was found within patches regarding the spatial distribution of soil resources, soil depth and soil penetrability were significantly higher ($p < 0.05$) in the center position where plants were growing, than at the windward side where plants were not found to grow, or at the leeward edge of the patch, upslope or downslope. This pattern was similar at all three sites, with the exception of soil depth at Cataract Creek Basin, where no significant differences were found between effective soil depth and location (Table 3). Even though Cataract Creek Basin did not show significantly different effective soil depth in the patch center from other patch locations, it still had a higher mean than other patch locations. Intense wind speeds that may influence seed dispersal and germination (that would initiate positive feedback effects), combined with a high slope gradient, could cause the lack of significant variation in soil depth with microsite position at Cataract Creek Basin, but positive feedback mechanisms between plants and soil are likely present.

Although not addressed in this study, a number of field-based studies and empirical and simulation models of site suitability conducted on the relationship between tree advance and soil factors such as soil texture, soil nutrients (Malanson and Butler 1994), and seed rain (Malanson 1997) at treeline in Glacier National Park have shown that areas exist within the study sites where trees could grow but do not (Malanson et al. 2002; Butler, Malanson, and Resler 2004). Variables such as soil depth and texture have been studied in Glacier National Park in light of alpine treeline advance. Alpine environments typically have low soil moisture potential because they are often poorly defined (Holtmeier and Broll 1992) and therefore soil depth could presumably limit tree growth because it would limit the amount of water available for seedling

growth (Cairns and Malanson 1998). However, Malanson et al. (2002) illustrated that effective soil depth does not control the spatial pattern of treeline advance at alpine treeline in GNP, nor do soil nutrients vary at the scale of individual seedling establishment.

*Link B: Regional Climate (Box 1) to Conifer Establishment, Conifer Mortality, and Conifer Growth (Box 2)*

The majority of research on treeline emphasizes the influence of macroscale climatic factors on treeline position. Snow, temperature, and wind direction are among the variables most closely connected with treeline dynamics. Related to these macroscale factors are mesoscale gradients, such as elevation, that also influence the biotic characteristics of treeline.

Snow is a dominant factor affecting patterns of alpine vegetation (Walker, Billings, and DeMolenaar 2001; Alftine, Malanson, and Fagre 2003). Both macro- and microtopography can influence the distribution of snow and snow melt; this in turn has a profound influence on seedling survival and patterns of vegetation, and can affect conifer seedlings at treeline both positively and negatively. The importance of precipitation in the form of snow and rain is the moisture thereby provided to soil. At alpine treeline in mid to upper latitudes, snow is a particularly important moisture source given its seasonal dominance. An indirect effect of wind on seedling establishment is its effect on the distribution of snow, the result of which is controlled by the interaction of topography and climate vectors (Körner 1999; Walker, Billings, and DeMolenaar 2001). If a seedling is buried by snow, it is insulated from extreme winter temperatures and temperature fluctuations that result in freezing and thawing. Additionally, snow cover can protect a seedling from physical damage due to wind and ice-blasting (Walker, Billings, and DeMolenaar 2001). Conversely, vegetation can collect deep, late-lying snow drifts. If melt of these drifts is too late, growing season can be reduced and vulnerability to snow molds and competition with shrubs can increase (Arno and Hammerly 1984; Spittlehouse and Stathers 1990; Körner 1999).

Temperature in general and summer warmth in particular are primary factors that determine how a tree grows and reproduces (Wardle 1974; Tranquillini 1979). Therefore, changes in summer temperature are crucial in determining treeline elevation fluctuations over time (Innes 1991). The response of a tree to temperature is species specific, and determines its upper and lower elevational range (Arno and Hammerly 1984). For treeline species, increasingly cold temperatures means that the growing season shortens and the potential for frost damage increases (Arno and Hammerly 1984). In the absence of geomorphic disturbance, it is the factor that determines the ultimate altitude to which trees can grow (Arno and Hammerly 1984). In the Northern Hemisphere, the upper limit of tree growth is frequently cited as corresponding roughly to the $10°C$ isotherm for the warmest month of the year (Daubenmire 1954; Arno and Hammerly 1984).

High wind speeds characteristic of high mountain environments are related to topographic complexity, rather than to the effects of altitude (Barry 1992). Wind interacts with relief at numerous scales, affecting boundary layer conditions that ultimately influence heat loss, evaporative cooling, and the distribution of snow and precipitation (Körner 1999). Macro-, meso-, and microscale topography may jointly determine wind distribution and speed at a particular site and, as a result, influence the pattern of conifer establishment (Holtmeier and Broll 2005).

At Lee Ridge, the pattern is characterized by elongated krummholz islands, oriented parallel to the prevailing westerly wind, with windward to leeward establishment of successively younger trees (Bekker 2005). This pattern is suggestive of the importance of wind-mediated switches in producing pattern (Alftine and Malanson 2004). At Cataract Creek Basin and Divide Peak, unidirectional, wind-mediated treeline patterns are not so obvious because prevailing wind directions are not as consistent. At Cataract Creek Basin, for example, wind blowing over the pass from the top of the cirque headwall converges with winds originating from the lower valley. At Divide Peak, wind is channeled around the peak, converging with northwesterly winds away from the base of the peak. As a result, patches at these treeline sites are roughly triangular-shaped, rather than linear.

Macroscale topography results in variation in patch density and species richness with elevation and wind exposure. At Cataract Creek

Basin for example, no significant correlation was found between patch density and elevation, but descriptive observations indicate that conifer density becomes greater with increasing elevation. Increasing elevation at Cataract Creek Basin results in increased protection both because the site is located at the base of a cirque headwall away from the direct impact of the wind and because microtopography in the form of terrace riser angles is higher on these steep slopes. Due to a prominent wind from over a pass at the top of the headwall, treeline appears to be advancing by converging at areas of exposure from closed treeline sources downslope and higher elevation sites. Additionally, topographically-channeled wind is likely an important carrier of seed from subalpine meadows on the other side of the pass. However, at Divide Peak, a strong negative correlation characterizes the relationship between elevation and density. This finding indicates that elevation, a proxy for temperature, is not an equally important controlling variable in patch number among all three sites and suggests the importance of other controlling variables, such as wind exposure, in patterns of tree establishment. A significant, but weak correlation between elevation and species richness was found only at Lee Ridge ($r = -0.36$, $p < 0.05$). Here as elevation increases, treeline becomes more exposed. No other study sites recorded a significant relationship between species richness and elevation. At the highest portion of the ridge, even boulders do not serve as sufficient shelter. The exposure is too great to support a single conifer, let alone rich species diversity. These observations and findings highlight the important notion that the nature of treeline advance may be multidirectional, depending on areas of exposure.

Among the three sites examined in this study, the interplay between micro- and macroscale topography and the position of conifer establishment sites are important variables in determining the species richness of a site and growth of conifers at that site. Whereas all sites share similar microtopography, macrotopography is quite different and this configuration has an important influence on the characteristics of conifer establishment at the alpine treeline ecotone. This biogeomorphic connection means that initial treeline response to changing climates will differ geographically according to microtopography.

### Links $C_1$ and $C_2$: Conifer Establishment, Conifer Mortality, and Conifer Growth (Box 2) to Treeline Advance and Treeline Retreat (Box 3)

Migration of climatically-controlled treeline, either as advance or retreat, is directly related to natural regeneration and climatic factors that determine the seed-producing capabilities of trees. Treeline advance upslope would indicate that climatic conditions favor seed years that result in both production and distribution of seed. The retreat of treeline would indicate that conditions are no longer advantageous to the survival of trees where they once were found (Tranquillini 1979).

As this study and others have clearly shown, geomorphic sites have the potential to become ideal locations for seedling establishment above treeline location through expansion of the resources available to trees. Rare seedling occurrence above current treeline elevations in the Medicine Bow Mountains (Germino, Smith, and Resor 2002; Smith et al. 2003; Hättenschwiller and Smith 2004) and Glacier National Park (Butler, Malanson, and Resler 2004) indicates sensitivity to climate, but is also indicative of the importance of positive feedback and positive plant interactions, such as facilitation, in seedling establishment in increasingly stressful abiotic environments (Callaway 1995; Callaway et al. 2002). Bekker (2005) also found evidence that the relative importance of positive feedback and climate varies over time with change in environmental conditions.

Landscape-scale theories of treeline cite an approximate threshold of the 10°C isotherm for the warmest month of the year as the approximate location of treeline. These theories, however, do not consider the fine-scale variability in location at which this threshold temperature can exist and at which elevation becomes a less useful predictor of biotic conditions as exposure increases (Körner 1998, 1999). Spatial variability in environmental conditions becomes increasingly important with exposure (Körner 1999); therefore, treeline can advance differently in different places, depending upon the availability of shelter. Thus the link $C_1$ (Figure 5) is particularly relevant to the pattern of treeline advance.

Scale linkage between micro- and macroscale patterns of treeline response to a changing environment is evident when considering that

macroscale patterns, such as measurable landscape scale advance of treeline on a mountain slope, of alpine treeline ultimately depend on the survival of individual seedlings and saplings (Germino, Smith, and Resor 2002; Smith et al. 2003).

## Conclusion

Scale is among the most fundamental concepts in geography. Researchers from all facets of our discipline understand the importance of choosing a scale of analysis appropriate to their level of inquiry. However, less is understood about the complex relationships among scale-dependent processes that influence observable and measurable landscape scale patterns.

This study emphasized the role of surface geomorphic features in linking scale at alpine treeline in Glacier National Park, Montana. The model presented here suggests that the characteristics and direction of treeline advance is likely to show different patterns at different places, depending on interactions among micro- and macrotopography. Shelter availability at each of these locations controls the initial patterns of treeline advance. All three study sites share similar shelter types, dependence on shelter for establishment above current treeline, soil characteristics, mortality patterns, and fine-scale establishment characteristics. Similarities among the sites are largely associated with microscale patterns and processes, and differences among the sites are likely related to macroscale influences, such as macrotopography. Changes across landscape boundaries in general, and theories of treeline dynamics specifically, should consider the importance of surface features in structuring patterns of change. Despite the emphasis on treeline, the conceptual framework presented in this article has implications for many types of landscape transition zones, and highlights the notion that thorough analyses of a landscape may benefit from multiscale evaluations. ∎

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